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Some Aspects of the Bionomics of Fish in a Brown Trout Nursery Stream

By C. L. Hopkins

Fisheries Research Division
New Zealand Marine Department

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Frontispiece: Lower part of the valley of the Hinau Stream, looking down stream.

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FOREWORD

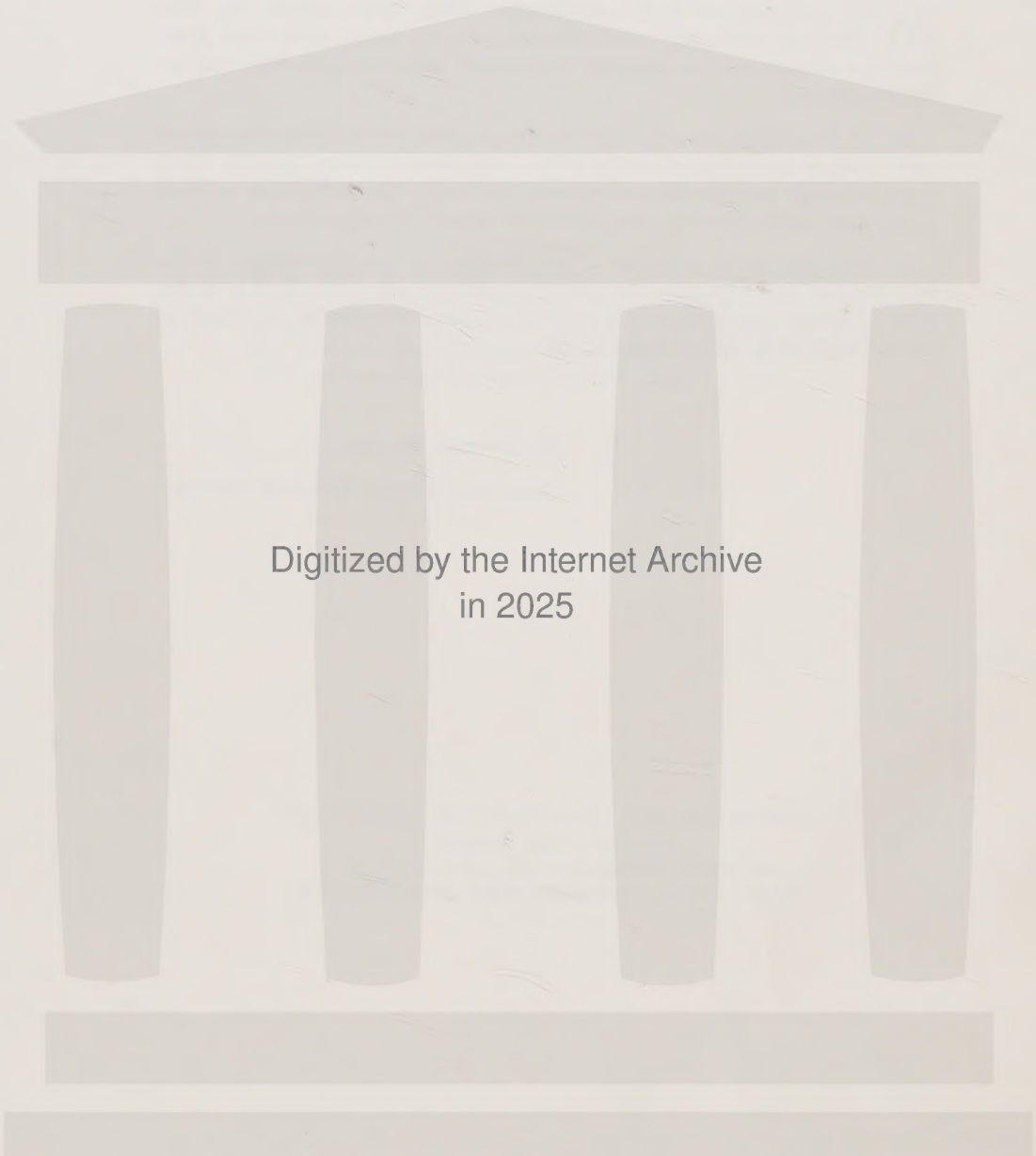
Many authors, scientists and anglers alike, have written of New Zealand trout and trout fisheries, yet few have made more than passing comment on the possible interaction between these fish and the native species.

In his detailed study of a trout nursery stream Mr Hopkins has shown that, though there appears to be little competition between species, there is considerable intraspecific competition for food. The availability of food is a major factor limiting the population density of each species.

In addition to its value as a contribution to our knowledge of the economy of small streams, this work is also of interest in that it shows that, at least in trout nursery areas, not all the native species are likely to be endangered by the introduced fish.

G. Duncan Waugh,

Director, Fisheries Research Division.



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INTRODUCTION

Most of the more comprehensive papers on the biology of trout in New Zealand (for example, Parrott 1932; Allen 1951; Smith 1959; Percival and Burnet 1963) have dealt with populations of immediate utility to the angler; there is little information on the interactions between trout and other fish. Percival (1932) and Allen (1951) indicated the possibility of feeding competition between trout and native species. Allen (1961) briefly discussed the predation of trout on bullies (Eleotridae) and smelt (Retropinnidae). Cairns (1942) discussed the problem of eel predation on trout. But there is no detailed study of a mixed population of salmonids and native fish aimed at evaluating the requirements of each species and their relations with each other. In other countries a number of papers have been devoted to this topic, particularly the feeding relations of trout with other fish (Hartley 1948; Thomas 1962; Maitland 1965; Straskraba, Cihar, Frank, and Hruska 1966).

To fill an apparent gap in research this bulletin describes some aspects of the biology of immature trout in a small nursery stream containing no resident adults. The field work was carried out between October 1964 and June 1967, and comparative observations can therefore be presented of virtually three isolated generations of trout, since the population turnover is annual.

The major purpose of the work is to describe the density, growth, and food requirements of the trout population and to examine its ecological relationships with other species of fish and invertebrates sharing the same environment.

The fish population described consists of brown trout (*Salmo trutta* L.), the bully *Philypnodon breviceps* Stokell, and the eels *Anguilla australis schmidti* Phillipps and *A. dieffenbachi* Gray. The trout are almost all juveniles which spend less than 12 months in the stream. The only adults entering the stream belong to the breeding stock, which ascends from larger rivers in late May, June, and July of each year to spawn, though there are a few small adults in the headwaters. The other fish species can be regarded as essentially resident, since several age groups are present throughout the year, though, of course, there is a gradual turnover of the migratory eels.

THE LOCALITY

The study was carried out in the eastern foothills of the Tararua Range, about 8 km west of Carterton in the Wairarapa district. The area is drained by the Hinaki Stream, a tributary of the Mangatarere Stream, which is itself part of the Waiohine River sub-system (fig. 1).

The main valley of the Hinaki consists largely of sheep and dairy cattle pasture, crossed by tree belts of *Pinus radiata* Don and *Cupressus macrocarpa* Hartweg. The upper courses of the Hinaki and its main tributary, the Hinau, run through narrow, steep-sided valleys of rough pasture, with large areas of scrub, fern, and regenerating forest. The hills in the area, which form a series of ridges, are of sub-metamorphic sandstones (greywacke) and rise to about 450 m above mean sea level. The soils of the Hinau valley are mainly very thin and are closely underlaid by alluvial gravel. In the main Hinaki valley a deeper, more fertile soil predominates.

The field work was done between the confluence of the Hinau with the Hinaki (map reference: N.Z.M.S. 1, sheet N157, grid 999605) and a point further up each stream where it divides equally into two smaller, steeper tributaries (fig. 1). This point on each stream is subsequently called the forks. The study area includes 2.5 km of the Hinau and 2.9 km of the Hinaki.

The Hinaki covers about 5 km from its sources at 250 m above m.s.l. to its confluence with the Hinau at 150 m above m.s.l. From its forks to the confluence the Hinaki flows southward through a wide valley which is largely pasture and it keeps to the low southern walls of the valley. Through most of the stream's meandering course the banks are low and vertical, seldom more than 1 m high and usually less than 0.5 m. The stream is up to 2 m wide and about 15 cm deep except in its many pools, which have depths of 40 to 50 cm. The bed, which is largely of coarse gravel and scattered larger stones, has an overall gradient of 1 in 70. Normal flows, measured near the confluence with the Hinau, are about 6 cusecs (0.17 m^3/sec) in winter and 1 to 2 cusecs (0.03 to 0.06 m^3/sec) in summer, but floods may exceed 20

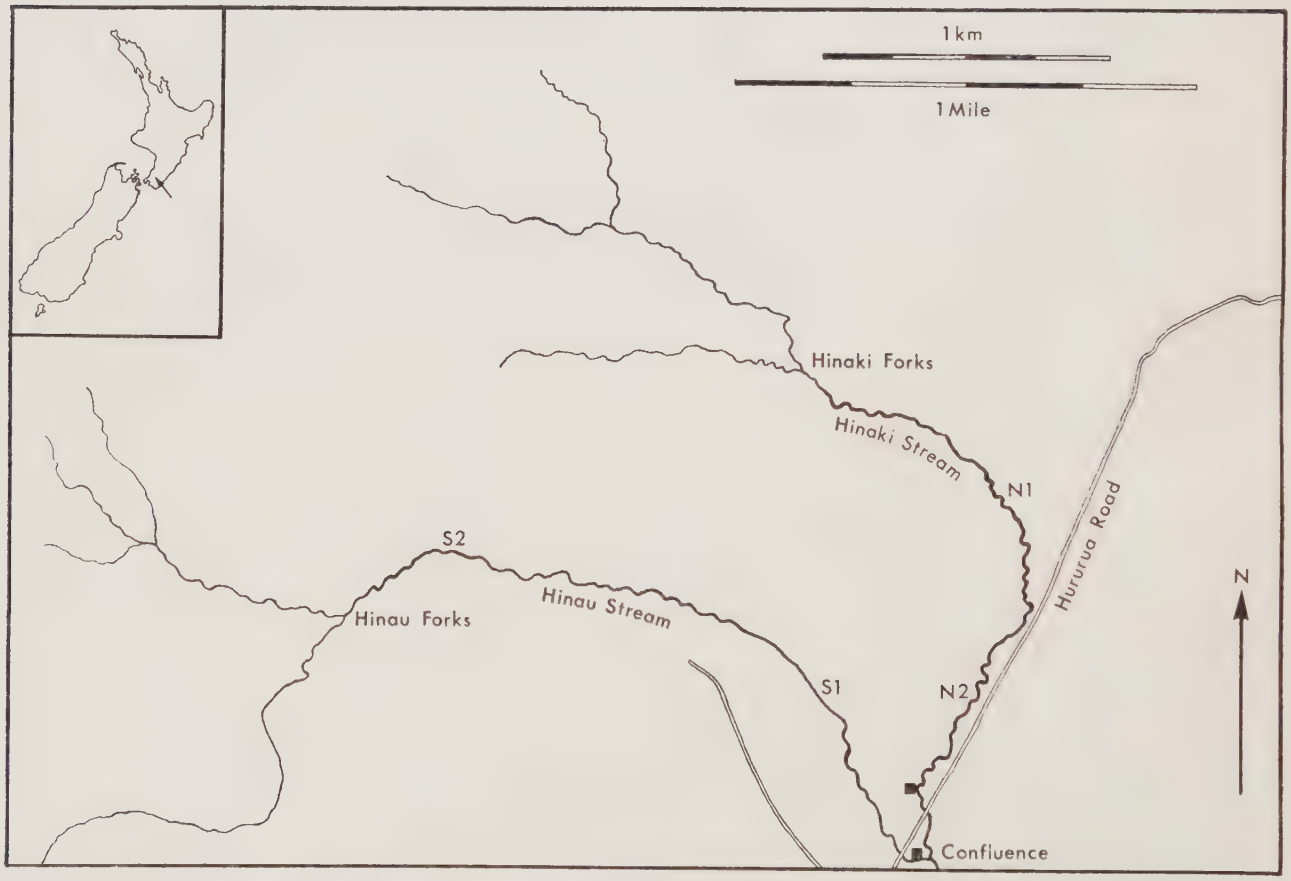

Fig. 1: The Hinaki and Hinau Streams, showing sampling stations. Positions of the fish traps are shown by black squares near the confluence.

cusecs (0.6 m^3/sec) for short periods. Temperature near the confluence varies between 4°c in winter and 19°c in summer.

The Hinau is about 4 km long and rises at 300 m above m.s.l. From its forks it flows at first through a high-walled narrow valley whose sides are covered with rough pasture, manuka scrub *(Leptospermum scoparium* Forster), and scrubby regenerating forest; on the valley floor are patches of manuka and tauhinu *(Cassinia leptophylla* Brown). The stream is 3 to 4 m wide, 15 to 20 cm deep, and fast flowing on a bed of coarse gravel and large stones. The valley widens out 700 m below the forks and its walls rapidly decrease in height toward the Hinaki. The land here is under pasture. At 1.1 km below the forks the stream becomes deeply entrenched in the wide valley floor, running between banks 4 to 5 m high for about 500 m, and in this region the surface water is reduced to a few discontinuous pools in summer. From 1.6 km below the forks the surface water is permanent, though the stream is smaller than in its upper regions, about 2 m wide and 20 cm deep, with pools up to 60 cm deep. The overall gradient is 1 in 45. Normal flows measured near the entrance to the Hinaki are about 8 cusecs (0.2 m^3/sec) in winter and 1 to 2 cusecs (0.03 to 0.06 m^3/sec) in summer, rising to 30 cusecs (0.8 m^3/sec) in floods. Maximum and minimum temperatures are the same as for the Hinaki at the points measured. The last 800 m of the Hinau receives organic pollution from a dairy herd which uses it as a watering place. The water is often turbid and the stream bed contains more silt than anywhere else in either stream. The algal growth which normally covers the stones in summer is much thicker in this region than elsewhere.

Four permanent sampling stations were used, two on each stream. Each station was 200 m long, which was enough for the various observations and sampling needed. Table 1 gives the position of the mid-point of each station from the confluence of the Hinaki and Hinau and shows the approximate area of stream bed.

Table 1: Distances from the Confluence to the Mid-points of Stations and Areas of Stream Bed

	Hinaki		Hinau	
	N1	N2	S1	S2
Distance from confluence (m)	2,000	900	600	2,000
Area (sq. m)	440	320	360	500

METHODS

During the first year fish and bottom fauna were sampled four times — in October 1964 and February, June, and October 1965. In subsequent years until June 1967 samples were taken in the same months, but an additional sample was taken in December. Sampling at station N2 was discontinued after June 1966.

For the first year up to and including October 1965 the trout population was sampled both at the permanent stations and in other parts of both streams. In June 1965 and 1966 the major trout-bearing sectors were fished right through, a distance of 2.7 km in the Hinau and 2.5 km in the Hinaki. Thereafter only the permanent stations were sampled.

BOTTOM FAUNA

The smaller benthic invertebrates were collected in a 1-sq-ft (930.25 sq cm) Surber sampler with a bag net of 0.5-mm mesh as described by Lagler (1956). Eight to 10 samples were taken from each station at every visit. They were stored in an aqueous solution of 4 percent formaldehyde. No attempt was made to sample specific micro-habitats, the collections being randomised as far as possible. All samples were taken in moderate to fast currents. The sampling method was not satisfactory for such fast-swimming forms as *Nesameletus* and *Oniscigaster,* which were clearly more abundant than the samples indicated.

At the laboratory the animals were counted and identified to the lowest taxonomic level possible. Densities of species in samples from the same station varied considerably. Standard deviations for total numbers ranged from 20 to 60 percent of the means, and for individual species they were generally between 40 and 100 percent of the means. Such large standard deviations (reviewed by Allen (1951)) reflect the great diversity of the stream environment coupled with the difficulty of making standard collections on a variable substrate in variable flow and depth. In some species, also, there were pronounced aggregations, for example, in *Helicopsyche* and the Sericostomatidae, which added to the variation.

Biomass was estimated from graphs of length against wet weight drawn for each species (or higher taxonomic group) from fresh material collected in February 1967. Only the soft parts of animals with cases or shells were weighed. Animals from subsamples of preserved collections were measured under the microscope with an eye-piece graticule and their lengths were converted into weights from the graphs.

ELECTRIC FISHING

Fish and crayfish were caught with a 240-volt, pulsed d.c., portable electric fishing unit, battery operated and delivering 150 to 200 pulses per second. This unit was designed by Mr K. F. Maynard, Fisheries Research Division. For sampling permanent stations the unit was connected to 200 m of cable so that the operator was able to cover 200 m of stream without having to move the power source. The positive electrode consisted of a ring of nickel-plated aluminium alloy attached to a wooden handle carrying switch gear, and the negative electrode was 10 m of braided copper wire laid along the stream bed. Sometimes the unit was used as a back-pack, the negative electrode being trailed behind the operator.

This equipment seemed to cause very little mortality, though some bruising occurred in trout and bullies, usually along the posterior part of the trunk. Probably less than 1 percent of bullies were killed, though no attempt was made to gather evidence of delayed mortality. No trout or eels were known to have died through electrical damage, but during hot summer weather there was a small loss (3 to 4 percent) of trout fingerlings which may have been caused by physiological damage attributable to the method of capture. Collins, Volz, and Trefethen (1954) recorded increased mortality of salmon fingerlings with pulsed d.c. at high temperatures.

Some trout fingerlings were found with a humpbacked appearance and all of them were appreciably smaller than usual for the time of year. This was attributed to electric fishing damage during a previous sampling period, as spinal damage can be caused by electric fishing (Hauck 1949).

Each permanent station was sampled by making three runs through 50 m of it with the positive electrode. Each run, which was started at the up-stream end, took about 45 minutes. Stunned fish and crayfish were usually picked up in a small wire-mesh dip-net, but any missed were caught in stop-nets, set at intervals through the section, as they drifted down stream. All species were collected together. The catch from each run was kept in separate live boxes so that numbers and measurements for each consecutive run were known.

Several workers (for example, Schuck 1945; Holton 1953) have tested the efficiency of electrical sampling from the proportion of a known number of marked fish subsequently recaptured. Others (for example, DeLury 1951; Burnet 1952b) have based their estimates on the assumption that, if certain conditions

are met, the decreasing catches provided by repeated removal from the same area should show such a linear relationship that a point can be calculated at which the whole population has been removed. Zippin (1956, 1958) designed a simple procedure based on this method for estimating populations of small mammals, sampling being done with traps. This procedure appears applicable to the present study and was used.

In Zippin's method two conditions are assumed: (1) that the probability of capture during each sampling is the same for each animal, and (2) that the probability of capture of each animal remains constant from one sampling to the next. In this study the ease with which the animals were caught differed considerably between species and between sizes, but the first condition was met by keeping species separate in the calculations and by estimating each species under different size categories. The second condition was almost certainly not fully realised in most samples because reduction in numbers increased the ease with which the remainder could be seen and caught, but provided the catches from the second and third runs formed only a small fraction of that from the first (which usually happened), the inaccuracy of population estimate was unimportant.

Many of the samples, when divided into appropriate size groups, proved too small for reliable estimates of numbers to be made. Relationships of total catch to total estimated populations have therefore been calculated for the largest samples and are assumed to apply to the rest. These figures (table 2) have been used to estimate the total populations present at each sampling period. The eels were originally divided into four sizes (both species combined), but the estimated proportion sampled varied from 0.92 to 0.99, with no evident relation to size; so mean estimates have been recalculated for all eels combined.

The sampling appears to be at least as efficient as found by other workers using similar methods. Schuck (1945) obtained a 50 percent recovery of trout under 100 mm, which rose to 95 percent for adults of over 200 mm. Holton (1953) estimated a 97 percent capture of trout over 90 mm long and 76 percent for smaller fish. Saunders and Smith (1954) found that 81 to 100 percent of all sizes of fingerling trout could be removed with three runs through a 50-yd section of a small stream. Burnet (1952a) estimated that at least 81 percent of all eels could be removed by three runs in small streams that he studied.

Table 2: Estimated Proportions of Fish and Crayfish Caught at Each Sampling, Based on Trial Runs Made in 1965

Species	Size category (mm)	Catch per run 1	2	3	Catch: total population
Philypnodon breviceps	20–39	48	29	19	.75
	40–59	121	30	15	.96
	59	108	17	4	.98
Salmo trutta	Fry	77	16	3	.98
	< 100	119	23	6	.98
	> 100	56	5	1	.99
Anguilla spp.	All sizes	74	22	11	.95
Paranephrops planifrons	6-10	87	46	20	.83
	10–19	72	26	9	.94
	> 19	39	8	4	.97

FISH TRAPS

In 1965 and 1966 traps were installed to catch adult trout migrating up stream to spawn, and both streams were fished from the forks down to the traps (a distance of about 3 km in both) to check any trout that had ascended before installation of the traps.

MEASUREMENT

Fish were narcotised with MS-222, a drug from which they recovered quickly when they were returned to fresh stream water, and were measured in the field with a measuring board. Lengths of trout were taken from the tip of the snout to the centre of the tail fork, and lengths of bullies and eels were taken from the tip of the snout to the centre of the convex border of the tail. Crayfish were measured with vernier callipers from the back of the eye socket to the mid-dorsal posterior border of the carapace. Weights of fish and crayfish were estimated from length; the weight to length relationship of trout was calculated from data in Allen (1951) and that of eels from Burnet (1952a). Series of bullies and crayfish were weighed fresh at the laboratory, and logarithmic plots of weight against length were drawn up as standards.

GUT ANALYSIS

Fish for gut analysis were caught outside the sampling regions and were killed and placed in preservative immediately. At the laboratory the fish were measured and the stomachs removed for examination. All food items were counted and measured or their lengths were estimated if they were broken up. Organisms in the stomachs of trout and bullies were usually whole and the necessary counts and measurements easily made. The gut contents of eels tended to be much more fractured, and much approximation was inevitable in estimating numbers and sizes of organisms.

The weight of food in the stomach was estimated as fresh weight from the same plots as were used for the general benthic and fish fauna.

THE BENTHIC FAUNA

SMALL INVERTEBRATES

Small invertebrates here include all forms collected by the Surber sampler. The species collected in the two streams during the study are listed in table 3 with an approximation of their abundance.

Numbers

The bulk of every collection consisted of *Deleatidium* spp., *Olinga feredayi* McLachlan, and *Pycnocentrodes* sp., but several other species that occurred in all or nearly all samples were also numerically important, for example, *Coloburiscus*, *Pycnocentria*, *Helicopsyche*, *Hydropsyche*, several Rhyacophilidae, Elmidae, and *Austrosimulium*. A few rare species were atypical of the habitat: *Cruregens fontanus* Chilton is a member of the subterranean interstitial fauna, and the hemipteran *Sigara arguta* (White) is more commonly found in pools and backwaters. The Dixidae are not part of the bottom fauna at all, as their larvae live at or near the water surface.

Most of the benthos is clearly made up of the two insect orders Ephemeroptera and Trichoptera, which numerically formed over 75 percent of the fauna and contributed 40 to 50 percent of the species. The two orders consist largely of grazing animals, but the Trichoptera also provide the most important groups of invertebrate predators, the Rhyacophilidae and Hydropsychidae.

The larvae of both Elmidae and Chironomidae were commoner in the summer than in other seasons, and adult Elmidae were present only in December and February, but most forms were equally numerous at all seasons. Of the insects most species of Trichoptera (see Mosely and Kimmins 1953) and Ephemeroptera (see Phillips 1930a, 1930b) are on the wing for several weeks; so the earliest instars of the new generation appear before the disappearance of mature larvae or pupae through emergence. The densities of the 12 most important groups (table 4) show some differences between the stations from October 1964 to October 1966. The groups shown are chosen partly

Table 3: List of Species Taken in All Samples

	Abundance
Tricladida	
Dugesia montana	++
Nematomorpha	
Gordius pachydermis	+
Annelida	
Oligochaeta	+++
Mollusca	
Pisidium aucklandica	+
Potamopyrgus antipodum	+++
Latia neritoides	+
Crustacea	
Ostracoda	+
Paracalliope fluviatilis	+
Cruregens fontanus	+
Ephemeroptera	
Ichthybotus hudsoni	+
Oniscigaster wakefieldi	+
Ameletopsis perscitus	+
Coloburiscus humeralis	++++
Nesameletus sp.	+
Deleatidium cromwelli	+
Deleatidium spp.	+++++++
Zephlebia cruentata	++
Zephlebia sp.	+
Plecoptera	
Stenoperla prasina	+++
Austroperla cyrene	++
Zelandoperla maculata	+++
Zelandobius sp.	+
Aucklandobius sp.	+
Megaloptera	
Archichauliodes diversus	+++

	Abundance
Hemiptera	
Sigara arguta	+
Coleoptera	
Elmidae	++++
Antiporus strigosulus	+
Trichoptera	
Polyplectropus sp.	++
Plectrocnemia maclachlani	++
Dolophilus stenocerca	+
Olinga feredayi	+++++
Pycnocentria evecta	++++
Pycnocentrodes sp.	++++
Beraeoptera roria	+++
Oeconesus maori	+
Helicopsyche sp.	+++++
Hudsonema amabilis	+
Oxyethira albiceps	++
Hydropsyche spp.	+++
Hydrobiosis umbripennis	+++
Hydrobiosis parumbripennis	+++
Hydrobiosis soror	+++
Psilochorema leptoharpax	+++
Psilochorema sp.	++
Neurochorema confusum	++
Costachorema xanthoptera	+
Diptera	
Tipulidae	+
Dixidae	+
Austrosimulium sp.	+++
Chironomidae	+++
Stratiomyidae	+
Anthomyiidae	+
Tabanidae	++

+++++++	Collection mean > 100, present in all samples.
++++++	Collection mean 50-100, present in all samples.
++++	Collection mean < 50, present in all samples.
+++	Collection mean < 50, present in 50-90 percent of samples.
++	Collection mean < 50, present in 10-49 percent of samples.
+	Collection mean < 50, present in 10 percent of samples.

At S1 a large fraction of the biomass was contributed by the Oligochaeta, which were fairly insignificant in numbers. Although the two large predators *Stenoperla* and *Archichauliodes* constituted only 0.5 to 1.0 percent of the benthic community by number, they made up 8 to 10 percent by weight.

Total biomass was distinctly lower at S1 than at the other two stations listed, and it was highest at N1. The low number and weight of benthic fauna at S1 probably resulted from the silt and organic pollution there, as it was the main watering place for a large herd of dairy cattle.

CRAYFISH

Density

Although part of the benthic invertebrate fauna, crayfish (*Paranephrops planifrons* White) are treated separately, because they are far larger and were collected with the electric fishing unit at the same time as the fish. Many young crayfish below 6 mm carapace length (C.L.) appear from December to February, but as very few were caught, the count for samples taken in these 2 months provides an inaccurate measure of their density if it is recorded unmodified. The numbers of juveniles of the 0+ age class for December and February were therefore estimated from the probable number of eggs produced in the previous winter. Since very few female crayfish of breeding size in the June samples had obviously lost eggs and dependent young, the number of young eventually released was considered to be equal to the number of eggs calculated from fecundity data in Hopkins (1967a). December was taken as the first month in which young (between 3 and 4 mm C.L.) were present. The greatest densities of crayfish occur in December and February, when the new 0+ age class is present in large numbers (table 6). Thereafter the populations are reduced until the next year's release of young crayfish.

Table 6: Estimated Number of Crayfish at Each Station at Each Sampling Period

	S1	S2	N1	N2	
Oct 1964	96	141	88	90	
Feb 1965	*257**	*354*	*343*	*207*	
Jun 1965	108	53	161	118	
Oct 1965	47	33	102	72	
Dec 1965	*610*	*262*	*777*	*266*	
Feb 1966	*434*	*182*	*678*	*187*	
Jun 1966	124	117	408	109	
Oct 1966	55	83	168		
Dec 1966	*631*	*364*	*1,088*		Discontinued
Feb 1967	*460*	*247*	*826*		
Jun 1967	124	153	297		

*Figures in italics include estimates of uncaught young of the year.

Table 7: Estimated Total Weight (g) of Crayfish at Each Station at Each Sampling Period

	S1	S2	N1	N2	
Oct 1964	306·5	568·9	224·3	239·1	
Feb 1965	322·5	602·2	419·6	232·2	
Jun 1965	426·7	220·8	644·9	205·6	
Oct 1965	230·3	128·3	596·8	269·5	
Dec 1965	137·8	65·0	629·3	306·0	
Feb 1966	295·9	193·8	603·3	173·6	
Jun 1966	405·6	438·2	1,199·7	318·4	
Oct 1966	217·4	259·5	557·8		
Dec 1966	549·6	419·4	907·1		Discontinued
Feb 1967	489·6	336·4	548·2		
Jun 1967	459·5	743·6	1,034·7		

Three to four age classes of crayfish were present (Hopkins 1967b). In winter only 3 to 4 percent of the population consisted of breeding females, most of them being in their third year. The production of eggs and young was fairly small, though obviously adequate to maintain the population, and the estimates of egg production at the four stations varied from about 200 to about 1,000.

Biomass

The wet weights of crayfish (table 7) have been estimated from logarithmic plots of length against weight in the same way as those for the smaller invertebrates. The estimated weights of uncaught juveniles in the December and February samples are included in the tables, though, in fact, they make little contribution to the total biomass.

Maximum total biomass is usually reached in June, when the 0+ age class is still large and the mean size has reached a level at which it is gravimetrically an important part of the population. Growth is much reduced in winter (Hopkins 1967b), but mortality is high, and the biomass therefore tends to fall from its June maximum to October, after which increased growth causes an upswing. As can be seen from table 7, this pattern is by no means constant, probably because of varying mortality and growth among different age classes which themselves vary in strength from year to year.

THE FISH POPULATION

TROUT

The trout population is largely transitory and the two study streams act as nurseries for the immature stages, most of which leave before the beginning of the next spawning season in late May. The adults are present from the end of May to the beginning of July.

A few small trout occurred in the headwaters of the Hinau above the forks, outside the study area.

During the study spawning adults did not move much more than 2.4 km up stream from the road bridge on the Hinau and 2.7 km up stream from the road bridge on the Hinaki (fig. 1). This extent of up-stream migration was estimated from the distribution of fry in October, none being found further up stream.

Later in spring the fingerlings appeared to spread up stream beyond the original extent of the fry — another 600 m in the Hinau and rather less in the Hinaki — possibly in response to high density where the fry were produced. Kalleberg (1958) has shown by tank experiments that trout fry and fingerlings establish territories, the fry almost as soon as they emerge from the redd. He found that fry territories covered about 2.3 sq dm and fingerling territories extend up to 1 sq m. This could account for a movement of fish into previously unoccupied areas up stream and explain the more pronounced movement in the Hinau, which held a bigger population of young trout in at least 2 years of the study.

The 1965 spawning run of adult trout consisted of 19 males and 15 females in the Hinaki and 18 males and 21 females in the Hinau. The latter run was earlier, 26 adults having passed up the Hinau before the first one entered the Hinaki. From age rings on 20 sets of scales it appeared that most migrating fish were 3-year-olds. Four large males (469, 448, 490, and 513 mm) were 4-year-olds, two of which showed from spawning marks on the scales that they had spawned the previous year. Average length of the adults was 427 mm, the range being 301-560 mm.

The 1966 spawning run was greatly reduced, only five fish ascending the Hinaki and seven the Hinau, and few fry were found in the following spring and summer.

Egg and Fry Production

Since the number of females spawning in both streams is known for 1965 and 1966, the number of eggs laid each year can be estimated. Although neither Brown and Kamp (1942) nor Horton (1961) found any correlation between size or age of females and the number of oocytes in mature ovaries, both Allen (1951) and Cooper (1953) describe a systematic rise in the number of oocytes with increasing size of mature fish. The size of fish ascending the two study streams included several larger than those examined by Allen; so for uniformity Cooper's results, which agree closely with Allen's, have been used to estimate egg production.

The 1965 spawning estimates were about 27,000 eggs in the Hinaki and 39,500 in the Hinau, and those for the very small spawning run of 1966 were 2,800 and 6,500 respectively. These figures refer to the mature oocytes in the ovary. Hobbs (1948) found that about 0.6 percent of eggs remained unshed after spawning and from work on several New Zealand rivers he estimated a mean loss of 10 percent of eggs in the redds through infertility and failure to hatch.

From the above figures the total number of eggs hatching in the two streams in 1965 was estimated (table 8). The table also shows the numbers of fry present in October 1965, estimated from thirty-two 2-m samples from various parts of the two streams. The figures for fry are based on an assumed 78 percent capture (in one run) during electric fishing. This figure for efficiency was based on repeated trial runs over 2-m lengths of stream and had a calculated error of $\pm$ 6 percent ($P = .05$).

Table 8: Estimated Numbers of Trout Eggs and Fry in the Hinau and Hinaki Streams for 1965

	Hinau	Hinaki
Number of females	21	15
Number of eggs hatched	33,700	23,000
Number of fry	10,440	5,940
Ratio fry : eggs	·31	·26

Spawning in the winter of 1966 was so little that subsequent fry estimates were meaningless. After escape from the redds the distribution of fry was so patchy that chance alone dictated their recovery in the sampling areas.

Mortality and Migration

From comparison of the estimate of fry present in October 1965, and the number of eggs hatched, it appears that considerable mortality occurred during the earliest free-living period, which was about 2 weeks, since the largest fry (34 mm) could attain this length in the time (Allen 1951). Presumably some mortality was due to predation, most likely from eels (Hobbs 1940), though 22 eels taken at an equivalent time in the previous year had no fish remains in their

stomachs. Other fry may have died from starvation caused by possible territorial fighting which resulted in excessive activity and too little time for feeding.

Table 9 presents the estimated trout populations (young of the year) in the two streams from October 1964 to June 1966. Figures for the October fry are based on an assumed occupation of 2.5 km of the Hinau and 2.7 km of the Hinaki. The older groups are calculated on occupation of 2.5 km of the Hinau and 2.9 km of the Hinaki. In February 1965 five samples taken from various stretches in the Hinau and six from the Hinaki were used to calculate total stream populations. For computation of the figures for that period in table 9 the streams were divided into sectors, each being centred on a sample representing trout density in that sector. This method was used because the distribution of fingerlings suggested that densities were highly variable. These samples themselves were taken from a length of about 25 percent of each stream. The June 1965 and 1966 estimates are based on numbers of fingerlings caught while the complete study area was being checked for spawning adult trout. The estimates for December 1965 and February 1966 have been computed from only the two permanent sampling stations on each stream.

Table 9: Estimated Trout Population in the Hinau and Hinaki Streams, 1964-66

	Hinau	Hinaki
Oct 1964	12,720	9,325
Feb 1965	1,434	936
Jun 1965	240	220
Oct 1965	10,440	5,940
Dec 1965	3,430	618
Feb 1966	1,575	610
Jun 1966	338	138

Table 10: Survival of Trout Fingerlings in Hinau Stream Above and Below the Barrier

	Upper sector		Lower sector	
	Population	Apparent survival %	Population	Apparent survival %
Oct 1964	4,072	100	6,106	100
Feb 1965	966	24	468	8
Oct 1965	3,341	100	5,011	100
Dec 1965	1,190	35	2,240	44
Feb 1966	1,000	30	575	11

The proportion of October fry remaining at subsequent periods of the year can be calculated from table 9. In February 11 percent of the 1964 year class were surviving in the Hinau and 10 percent in the Hinaki; by June the percentage had fallen to 2 in both streams. The pattern was exactly the same in the Hinaki for the 1965 year class, but in the Hinau 15 percent remained in February. In fact, the figures for February in the Hinau were low for both years because about 500 m of stream between S1 and S2 lost surface flow by November, so that the trout left after November were fewer by that number originally inhabiting the summer drought zone. If allowance is made for the loss of these trout, the proportion remaining in the Hinau in February was 14 percent for 1964 and 19 percent for 1965.

Not all the drop in numbers was due to mortality, since the population was also reduced by movement of young trout out of the stream. Fortunately, mortality can be estimated in the Hinau population, for those fish up stream of the summer drought zone had no chance of escaping down stream until the stream flow became continuous in autumn. Changes in numbers must therefore have been due to mortality.

From the distribution of fry in October, estimates have been made of their numbers and apparent survival on either side of the summer drought zone (table 10). Fewer fry remained in the lower sector in February than in the upper sector, and the December survival was about the same in both sectors in 1965. As there appears to be no reason why survival should differ in the two sectors, it is assumed that the extra decrease in February numbers for the lower sector (16 percent in 1965, 19 percent in 1966) was due to down-stream movement. Furthermore, this movement began some time between December and February. True mortality must have been about 60 to 70 percent in both sectors from the October fry stage

Table 11: Mean Lengths (mm) of Young Trout, in Year Classes, for Each Sampling Period

	Hinau			Hinaki		
	1964	1965	1966	1964	1965	1966
Oct 1964	29·6 (240)*			28·4 (320)		
Feb 1965	90·0 (276)			82·4 (264)		
Jun 1965	130·6 (53)			124·1 (30)		
Oct 1965	138·2 (9)	28·8 (147)		141·5 (6)	31·5 (200)	
Dec 1965		59·2 (452)			66·8 (126)	
Feb 1966		90·6 (117)			103·3 (115)	
Jun 1966		124·6 (13)			135·3 (30)	
Oct 1966		145·2 (12)	29·0 (41)		—	—
Dec 1966			56·2 (24)			—
Feb 1967			86·0 (42)			97·4 (25)
Jun 1967			151·3 (20)			184·5 (4)

* Figures in parentheses are numbers measured.
— No fish were caught.

Table 12: Mean Lengths (mm) of Young Trout, in Year Classes, at Each Station for Each Sampling Period

	S1			S2			N1			N2	
	1964	1965	1966	1964	1965	1966	1964	1965	1966	1964	1965
Oct 1964	28·9 (63)*			31·0 (150)			28·3 (160)			28·5 (160)	
Feb 1965	91·6 (34)			88·4 (61)			82·8 (139)			86·5 (36)	
Jun 1965	—			127·0 (6)			116·4 (8)			130·5 (4)	
Oct 1965	—	27·6 (105)		139·4 (8)	30·0 (42)		141·5 (6)	31·5 (54)		—	32·5 (130)
Dec 1965	164·0 (3)	59·5 (164)			58·9 (288)		173·0 (2)	67·4 (104)			66·1 (22)
Feb 1966		90·2 (54)			90·9 (63)			100·7 (90)			105·9 (25)
Jun 1966		128·4 (5)			120·8 (8)			131·4 (9)			149·5 (14)
Oct 1966		139·0 (1)	29·0 (41)		145·7 (4)	—		154·0 (2)		} Discontinued	
Dec 1966			55·8 (21)		164·0 (2)	—		—			
Feb 1967			82·7 (25)			94·4 (6)		268·0 (3)	97·4 (25)		
Jun 1967			150·7 (8)			151·6 (12)		—	184·5 (4)		

*Figures in parentheses are numbers measured.
— No fish were caught.

to the February fingerling. According to the data for the upper sector in December 1965, most of this mortality took place before December. Allen (1951) found mortality highest in the first few months after fry left the redds.

In the Hinaki numbers fell by 90 percent between October and February in both years. Since trout could move freely throughout, mortality cannot be distinguished from down-stream dispersal. But in 1965-66 the estimated number of trout present was almost the same in December and February, which suggested that down-stream movement did not begin until after February. If this was so, the 90 percent fall in numbers from October fry was due to mortality. This death rate was 20 to 30 percent higher than in the Hinau, which might be expected, since the predator population (eels) was five to six times higher in the Hinaki than it was in the Hinau.

The 1966 year class was so small that no reliable estimate of number and mortality can be made.

Growth in Length

Young trout generally grew faster in the Hinaki than in the other stream, as shown from the mean lengths for each sampling period from October 1964 to June 1967 (table 11). Where data were collected from outside the regular sampling stations, these have been included in the calculations of the means.

All paired samples between the two streams were given t tests. The December and February means are significantly different in the two streams in all years at $P = .05$, but, except for June 1967, the means for June cannot be proved different. Except in October 1964 and February and June 1965 the Hinaki fingerlings maintained a higher growth rate than the Hinau fingerlings.

Data for the four separate stations (table 12) show that the Hinaki down-stream station (N2) tended to produce larger trout than the up-stream station (N1). In nearly all samples there were fewer trout at N2, the population tending to concentrate higher up stream; so again this may imply that growth is affected by population density. However, the mean lengths at N2 may have been increased by faster-growing trout from up stream moving down into N2. Nall (1930) stated that faster-growing sea trout smolts migrate earlier, and Hobbs (1953) found the same occurrence in lake trout smolts.

Throughout the study growth remained about the same in S1 and S2 until 1966-67. This was the year in which the trout population was very small, so that any differences in growth rate between one station and another were less likely to be related to density. Yet in February 1967 the mean length of trout at S1 was significantly lower than at S2. This may reflect

Table 13: Mean Weights (g) of Young Trout, in Year Classes, at Each Station for Each Sampling Period

	Hinau						Hinaki				
	S1			S2			N1			N2	
	1964	1965	1966	1964	1965	1966	1964	1965	1966	1964	1965
Oct 1964	·44			·50			·42			·43	
Feb 1965	11·65			10·42			8·74			9·92	
Jun 1965	—			31·17			24·30			41·93	
Oct 1965	—	·43		41·94	·48		42·70	·52		—	·56
Dec 1965	62·80	3·17			3·32		75·50	4·55			4·58
Feb 1966		11·20			11·84			16·90			18·17
Jun 1966		27·89			25·80			34·03			35·00
Oct 1966		38·30	·44		32·73	—		52·15	—	Discontinued	
Dec 1966			2·55		62·90	—			—		
Feb 1967			8·99			12·59			14·03		
Jun 1967			50·56			51·91			78·70		

— No fish were caught.

the temporary food shortage in the spring of 1966 in the lower part of the Hinau because of application of DDT to the hillsides above S1 (Hopkins, in prep.).

Growth in Weight

The mean weights of trout at the four stations throughout the study are shown in table 13. While trout remained in the two streams growth rate throughout the year (fig. 2) was not constant and was initially somewhat higher in the Hinaki than in the Hinau (as shown by the difference in slope of the curves in fig. 2). This was apparently due to a lead gained in the first few months of life, for the subsequent growth rate was not higher than it was in the Hinau.

EELS

Density

Both species of New Zealand eels were found in the study area, but they were much more abundant in the Hinaki, which offered better cover, in pools and undercut banks, than the Hinau. They were less frequent in the upper waters, particularly above the forks in both streams. *Anguilla australis schmidti* was commoner than *A. dieffenbachi* at all stations.

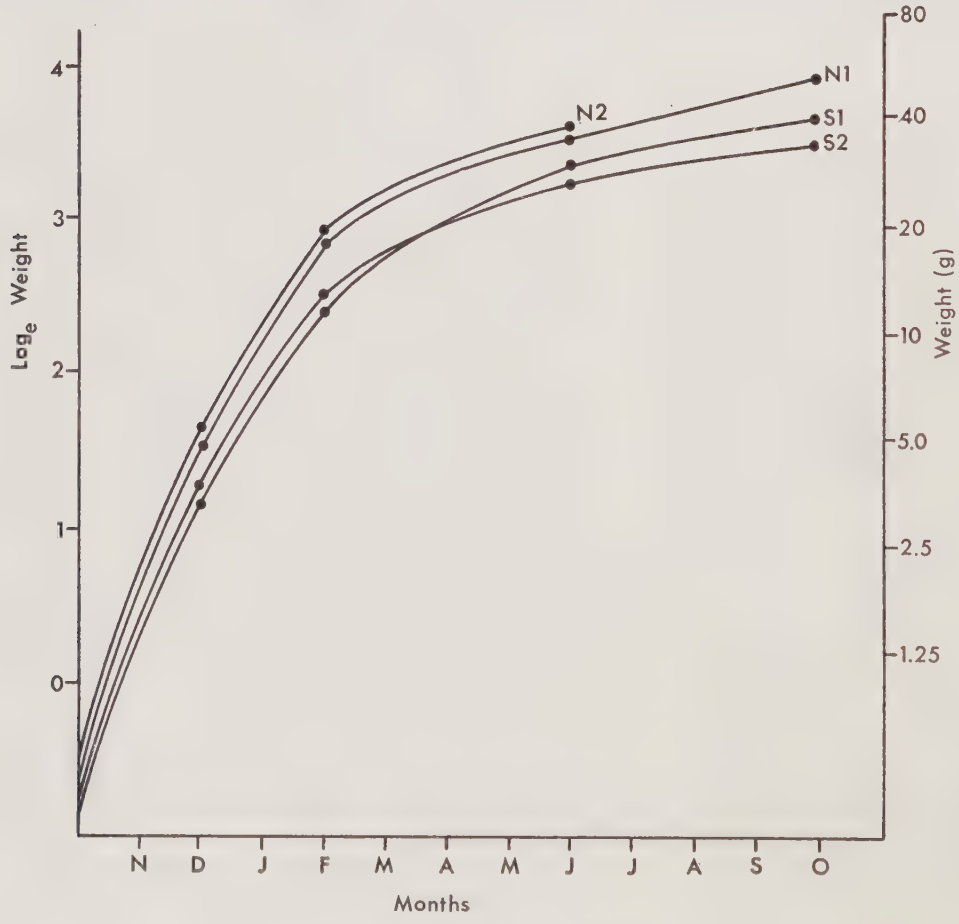

Fig. 2: Growth curves of trout at the four permanent sampling stations, October 1965 to October 1966.

Table 14: Estimated Number of Eels at Each Station at Each Sampling Period

	S1			S2			N1			N2		
	A.a	A.d	Total	A.a	A.d	Total	A.a	A.d	Total	A.a	A.d	Total
Oct 1964	13	3	16	22	21	43	77	25	102	77	59	136
Feb 1965	29	4	33	9	13	22	73	40	113	103	61	164
Jun 1965	5	2	7	4	5	9	40	23	63	67	23	90
Oct 1965	8	5	13	11	7	18	24	21	45	81	49	130
Dec 1965	14	2	16	9	2	11	44	40	84	70	47	117
Feb 1966	30	7	37	9	5	14	88	66	154	118	59	177
Jun 1966	15	4	19	20	12	32	81	41	122	73	59	132
Oct 1966	17	2	19	18	15	33	44	15	59			
Dec 1966	16	1	17	23	17	40	31	17	48	Discontinued		
Feb 1967	31	13	44	13	19	32	33	17	50			
Jun 1967	25	3	28	8	13	21	51	19	70			

A.a *Anguilla australis.*
A.d *Anguilla dieffenbachi.*

The density of eels of both species was not constant through the year (table 14), but frequently reached a peak in the summer (February) samples. This was due to the influx of young eels ascending the streams then. The size of the influx was very variable between stations and at some a February rise in numbers was not evident. This irregularity was probably due to distance from the sea. No mass migration of elvers was noted, the main movement having presumably spent its force before reaching the Hinaki and its tributaries. Juveniles entering these streams had already reached the end of their active migratory phase and were seeking cover in which to settle. Their numbers were therefore likely to be controlled by the space available down stream.

In general fewer eels were caught in June than at any other time of year. According to Cairns (1941), both species tend to hibernate, though some eels fed actively during winter. The estimated densities at the sampling stations during this period are subject to errors of unknown magnitude. Some comatose eels were more easily disturbed and captured than others, depending on the distance they had retreated into the stream banks or beneath loose gravel. It can be assumed that the populations in June were higher than indicated in table 14, the figures of which have been calculated only on estimated efficiency of catch of active fish. However, for present purposes the apparent reduction in numbers in winter is immaterial.

Adult eels migrate down stream in summer. This movement contributed to the decline in winter and spring, but the annual number of migrants was unknown. According to Cairns (1942), *A. dieffenbachi* is mature at about 850 mm and *A. australis* at about 750 mm. Less than 6 percent of *A. dieffenbachi* measured 850 mm or more at any single period, and no *A. australis* was longer than 500 mm. However, one of the latter species measured 389 mm in February 1965 and was in typical migratory colours. Such eels were very rarely caught and some probably move down stream before metamorphosis.

Age and Growth

Because few eels were caught at each station and a large number of age classes was presumed to be present, reliable knowledge of age and growth is difficult to obtain. No scales or otoliths were examined; nor were any eels marked. Length frequency analysis (Harding 1949) had therefore to be used to obtain the required information. Only the combined catch from N1 and N2 for February 1966 (fig. 3) was large enough to allow some measure of annual growth rate.

From the combined figures of these two samples the first three age classes of *A. australis* could be reliably identified, these making up 92 percent of the distribution. Young eels begin to move up stream in their third year and may take from 1 to 3 years to reach up-stream areas. The youngest year class in the February samples was therefore at least 3+ and possibly older. Its mean length was 132 mm. The two subsequent identifiable classes were of 179 mm and 210 mm mean length.

For *A. dieffenbachi*, present in smaller numbers, only the first two age classes were identified. Their mean lengths were very close to those of *A. australis*. The youngest age class was 129 mm long and the next age class was 170 mm. The two classes made up 62 percent of the whole sample and there was a much larger "tail" to the distribution than in the other species, probably containing a greater number of age groups.

Weight

Burnet (1952a) examined eels from several different sources and found the relationship between length and weight to be closely similar. It seemed reasonable, therefore, to apply his figures to obtain table 15, though his data refer to *A. dieffenbachi*. This species is slightly heavier for a given length than *A. australis* (Cairns 1941), and therefore there may be some over-estimates in the table.

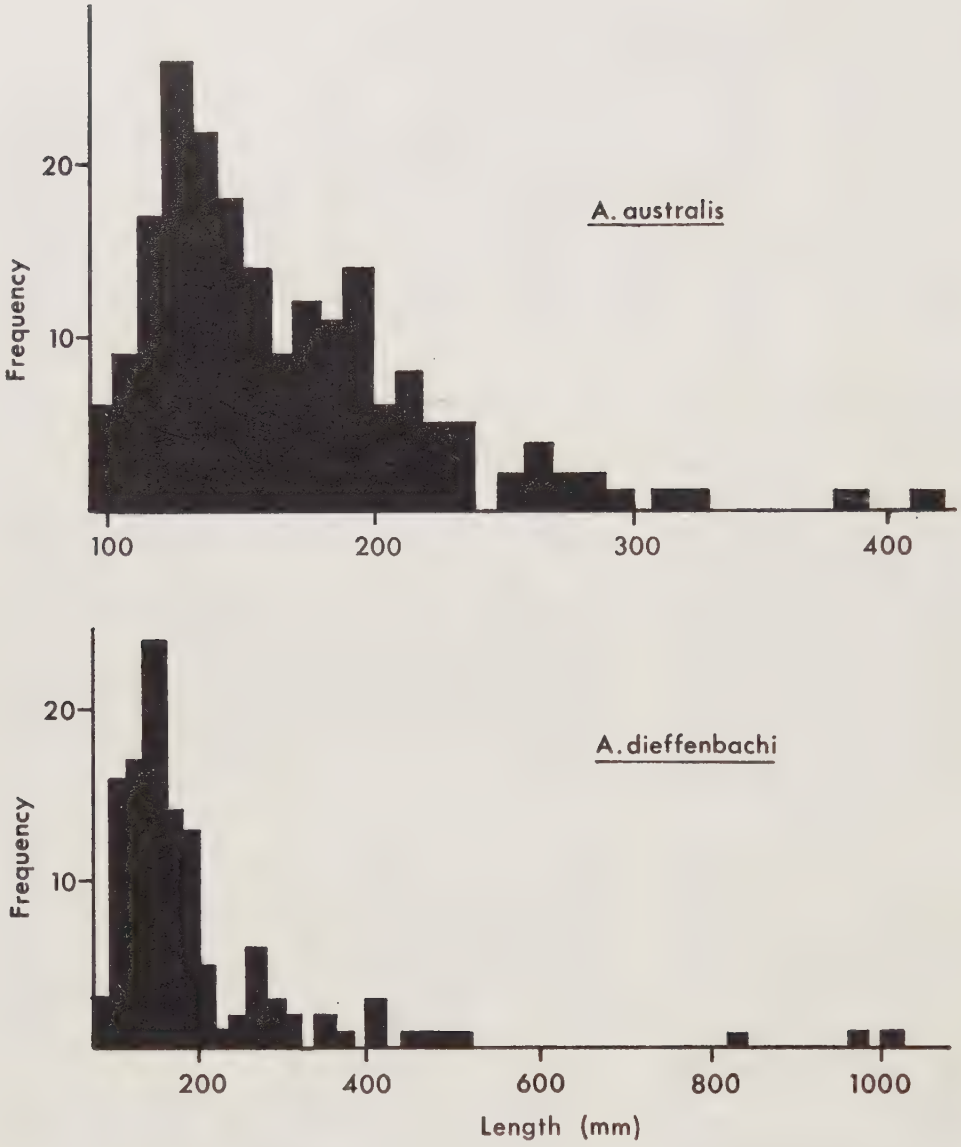

Fig. 3: Size composition of combined samples of eels taken from stations N1 and N2 in February 1966.

BULLIES

Density and Survival

Bullies (*Philypnodon breviceps* Stokell) occupy both streams up to and beyond the forks. Their numbers dwindle rapidly above the forks of the Hinau, and exploratory collecting in the south branch of the Hinaki showed that a few reach about 1 km above the forks. The density of fish varied widely in different parts of the two streams. At S2, in particular, the population was sparse, though bullies were abundant on either side of this station. The Hinau is unstable at S2, being braided in many parts and following a shifting course among loosely packed gravel. This instability is possibly the reason for the low numbers of bullies at the station.

Table 15: Estimated Weight (g) of Eels at Each Station at Each Sampling Period (Species Combined)

	S1	S2	N1	N2	
Oct 1964	2,736	4,995	8,364	10,244	
Feb 1965	2,868	1,386	14,285	10,457	
Jun 1965	1,171	593	2,720	4,155	
Oct 1965	2,011	1,496	4,001	6,138	
Dec 1965	1,278	616	12,424	6,088	
Feb 1966	2,540	904	5,093	11,503	
Jun 1966	1,521	1,112	6,283	7,642	
Oct 1966	1,007	3,369	6,096		
Dec 1966	1,173	4,900	3,367		Discontinued
Feb 1967	2,677	5,274	5,932		
Jun 1967	1,499	1,544	6,134		

The numbers of bullies inhabiting the two streams were not computed as was done with the trout, but there were probably more than 12,000 in each stream at the beginning of the breeding season (October).

Apart from the February samples, the estimated number of bullies at each station during each sampling period (table 16) were corrected from the

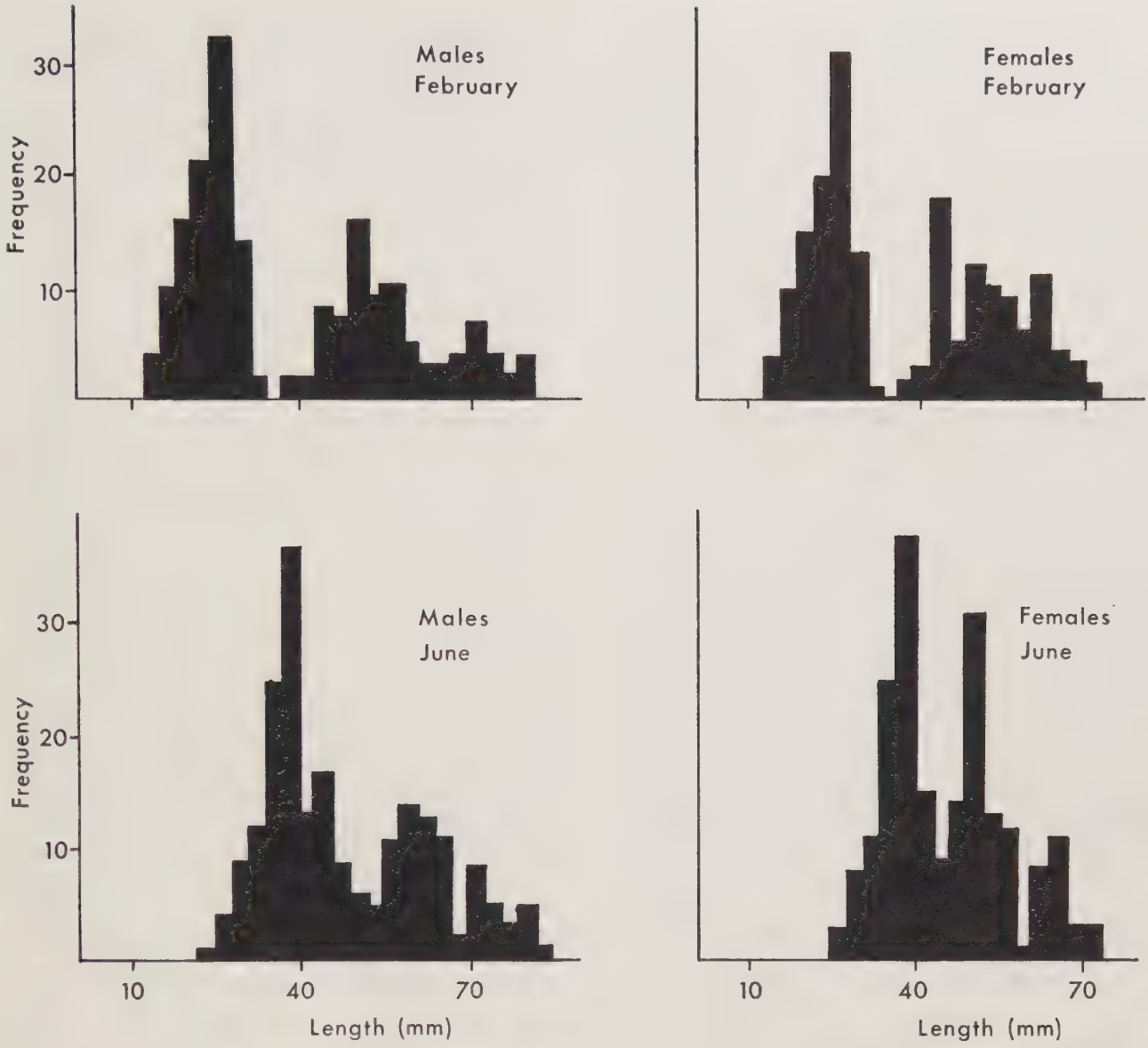

Fig. 4: Size composition of samples of bullies taken from station S1 in February and June 1965.

catch by the use of the data on catch efficiency, which has an error of about ± 8 percent. But it was obvious that most of the 0+ age class, present as fry in summer, were not appearing in the February samples. February fry numbers were therefore calculated by comparing the estimated numbers of fry hatched in spring and early summer with the numbers of this age class caught in June, when the fish were large enough to be sampled successfully. The breeding season extends from October to December, with an apparent peak in activity in November. In 45 nests examined in November and December 1965 the mean number of eggs was 378, range 50-850. Most nests

Table 16: Estimated Number of Bullies Present in 50 m at Each Station in Each Period

	S1	S2	N1	N2	
Oct 1964	213	205	322	140	
Feb 1965	*2,226**	*398*	*3,375*	*1,632*	
Jun 1965	400	58	369	169	
Oct 1965	237	112	277	156	
Dec 1965	146	27	162	89	
Feb 1966	*2,803*	*1,386*	*4,841*	*1,694*	
Jun 1966	634	127	502	123	
Oct 1966	361	102	327		
Dec 1966	284	96	274		Discontinued
Feb 1967	376	*882*	*4,267*		
Jun 1967	433	212	727		

*Figures in italics are based on estimations of eggs hatched (see text).

with fewer than 100 eggs showed evidence of damage and desertion. As each nest is guarded by a male bully, the number of nests can be estimated from the number of breeding males present, provided that there is an excess of females, which appeared to be so. This gave a range of 20 to 60 nests per 50 m from the October and December samples. Of the 45 nests examined 21 percent appeared deserted (mould-covered eggs or discoloured patches on the stone, which showed considerable loss of eggs) and this percentage was allowed for in computing the number of fry hatched. Eggs of *Gobiomorphus huttoni* (Ogilby) take 2 to 4 weeks to hatch (McDowall 1965), and since the eggs of *P. breviceps* are somewhat larger, 4 weeks has been assumed for development in *P. breviceps*. With the peak of breeding activity in November the starting date of the new year class has been placed at mid December for mortality computation.

Further calculation depends on an estimate of the decrease in numbers between mid December and June. The change in number of a population with time can commonly be expressed by the relationship $N_t = N_0 e^{-mt}$, in which N is the population after time t, N_0 the original population, m a parameter known as the instantaneous mortality rate, and e is the base of natural logarithms (Allen 1951). For each station m was calculated from the estimates of N_{Jun} and N_{Dec} ($= N_0$). By altering t thereafter a new value of N for February was calculated. This method is subject to two large errors. The first is in the estimate of fry hatching. The assumption has been made that one male corresponds to one nest throughout the breeding season. Apart from the possibility that not all adult males breed, some probably breed more than once. Moreover, the standard deviation of the mean number of eggs per nest was about 100, which allows a considerable variation in fry production. The second source of error arises from the assumption that the instantaneous mortality rate is constant from hatching to a period when the young are about 6 months old. In fact mortality is probably much higher at the beginning of the period than toward the end. This will have the effect of decreasing the numbers below the estimates set for February. The estimates of total numbers for February (in italics in table 16) are liable to large errors, but from the available data they seem reasonable.

All the samples showed a polymodal size structure (examples shown in fig. 4), and therefore the different age classes could be isolated by size-frequency analysis. Samples from only S1 and N1 were used, as they were largest (table 17).

Normally three classes appear in any one period, though a fourth may sometimes be found immediately after the breeding season (see the 1965 and 1967 figures for N1). In the calculation of figures for the two sexes of the 0+ age class the sex ratio was assumed to be about 1:1, as it is when this class is large enough to be sexed alive in the field (its first October and December). Among the older fish, however, there are evidently fewer males than females (table 17). The bullies come into breeding condition, judged from the appearance of their gonads, in their second year and some live long enough to breed again

Table 17: Estimated Numbers of Bullies, in Year Classes, Present in 50 m at S1 and N1 in Each Period

	S1 Males						S1 Females					
	1961	1962	1963	1964	1965	1966	1961	1962	1963	1964	1965	1966
Feb 1965		21	65	*1,028**				33	51	*1,028*		
Jun 1965		17	66	125				23	77	90		
Oct 1965		15	38	62				13	66	43		
Dec 1965		1	19	44				13	36	33		
Feb 1966			8	78	*1,308*				30	71	*1,308*	
Jun 1966			6	80	214				33	90	211	
Oct 1966			6	47	116				13	60	119	
Dec 1966			6	36	79				10	57	96	
Feb 1967			2	34	148	†			10	46	136	†
Jun 1967				29	132	28				28	193	23
	N1 Males						N1 Females					
Feb 1965	11	43	120	*1,504*			1	53	139	*1,504*		
Jun 1965		16	62	57				38	156	40		
Oct 1965		12	60	46				29	91	39		
Dec 1965		8	39	27				13	54	21		
Feb 1966			20	35	*2,353*				30	50	*2,353*	
Jun 1966			12	50	163				22	66	189	
Oct 1966			8	34	128				10	49	98	
Dec 1966			8	35	100				8	40	83	
Feb 1967				25	51	*2,058*			3	17	55	*2,058*
Jun 1967				15	75	277				15	85	260

*Figures in italics are derived from estimations of eggs hatched and from numbers of 0+ fish caught in June (see text).
†The 0+ class at S1 for February 1967 was not calculated, as numbers of this class caught in June 1967 were too small.

in their third year. More females appear to survive to a second breeding season than males, many of which may die through guarding nests.

The seasonal change in numbers in the first year of life in each generation is puzzling. In almost every sample there was an increase in numbers of 1-year-old fish in February, and there seemed no possibility of confusion with the new 0+ class, whose largest members were also present in small numbers in the February samples. Possibly the youngest generation migrates down stream to deeper water, though *P. breviceps* is not regarded as a migratory species (Stokell 1955; Woods 1963; McDowall 1965). If they migrate, they return up stream between December and June, and the numbers of fish in the age class decrease thereafter as expected. At least some of the 0+ age class remain in the sampling areas throughout the year. The movement, which is probably local, may be caused by shortage of suitable still or slow-flowing water for the young, the excess population consequently moving down stream to deeper water.

Growth

Mean weights for each age class in S1 and N1 are shown in table 18. The February values for 0+ fish are approximations computed from the mean daily growth from hatching until June. The mean weight per fish of a sample of bullies taken just when the yolk sac was resorbed was 0.6 mg and this is taken as the mid-December starting point for each year class.

The parity of growth apparently exhibited by the two sexes over the first 8 months of life (see 1964 and 1965 year classes in table 18) is largely artificial, since the young fish could not be sexed and were arbitrarily divided into two equal groups. But at the end of the second summer females were appreciably smaller than males and possibly lag behind earlier.

Growth curves drawn by eye between points plotted from data in table 18 (fig. 5 and 6) show an anticipated pattern for the first year of life, initially very high through summer, reduced considerably in the first winter, and rising again in spring and summer. In the adults growth is almost confined to summer, the winter retardation continuing through the spring breeding season.

FOOD

Numerical

The stomachs of 399 trout, 657 bullies, and 135 eels were examined. Almost all trout and bully stomachs contained food, but about a third of the eel stomachs were empty. Since there appears to be little difference in the diets of the two species of eel (Cairns 1942) and because of the fairly small quantity of ingested food available for examination, results for both eel species were combined.

Table 19 gives the numbers of each food organism as a percentage of the total number of organisms found (percentage composition) and the numbers of fish containing each organism as a percentage of the total number of fish (percentage occurrence) from October 1964 to June 1966. Subsequent samples were anomalous, as the fauna was temporarily affected by DDT (Hopkins, in prep.).

Only a few taxa are important as food. These include Oligochaeta, *Potamopyrgus*, *Deleatidium*, *Coloburiscus*, Sericostomatidae, *Hydropsyche*, Rhyacophilidae, and Chironomidae. This partly reflects their abundance in the benthos, but a number of other groups, such as the Elmidae, *Helicopsyche*, and *Aus-*

Table 18: Estimated Mean Weights (g) of Bullies, in Year Classes, Present in 50 m at S1 and N1 in Each Period

	S1 Males						S1 Females					
	1961	1962	1963	1964	1965	1966	1961	1962	1963	1964	1965	1966
Feb 1965		4·8	1·7	·2				2·7	1·4	·2		
Jun 1965		5·2	2·5	·6				3·3	1·7	·6		
Oct 1965		4·9	2·8	·7				3·4	1·6	·7		
Dec 1965		4·7	2·6	1·0				3·4	1·6	·8		
Feb 1966			4·5	2·0	·1				2·1	1·2	·1	
Jun 1966			4·8	3·0	·3				2·7	1·6	·3	
Oct 1966			4·6	3·3	·3				2·7	1·9	·3	
Dec 1966			4·9	3·4	·7				2·8	2·0	·7	
Feb 1967			5·9	3·8	1·1	·1			3·2	2·2	·9	·1
Jun 1967				4·7	2·8	·3				3·3	1·8	·3
	N1 Males						N1 Females					
Feb 1965	5·1	3·0	1·1	·1			3·4	2·1	1·1	·1		
Jun 1965		4·8	2·1	·3				2·7	1·4	·3		
Oct 1965		4·3	2·2	·4				2·7	1·5	·4		
Dec 1965		4·4	2·2	·6				2·6	1·5	·6		
Feb 1966			3·0	1·6	·1				2·6	1·5	·1	
Jun 1966			4·4	3·3	·3				3·2	1·9	·3	
Oct 1966			4·6	3·2	·5				3·8	2·2	·5	
Dec 1966			4·9	3·1	·8				3·8	2·3	·8	
Feb 1967			4·9	3·2	1·1	·1			3·9	2·6	1·1	·1
Jun 1967				4·0	2·8	·2				3·5	1·7	·2

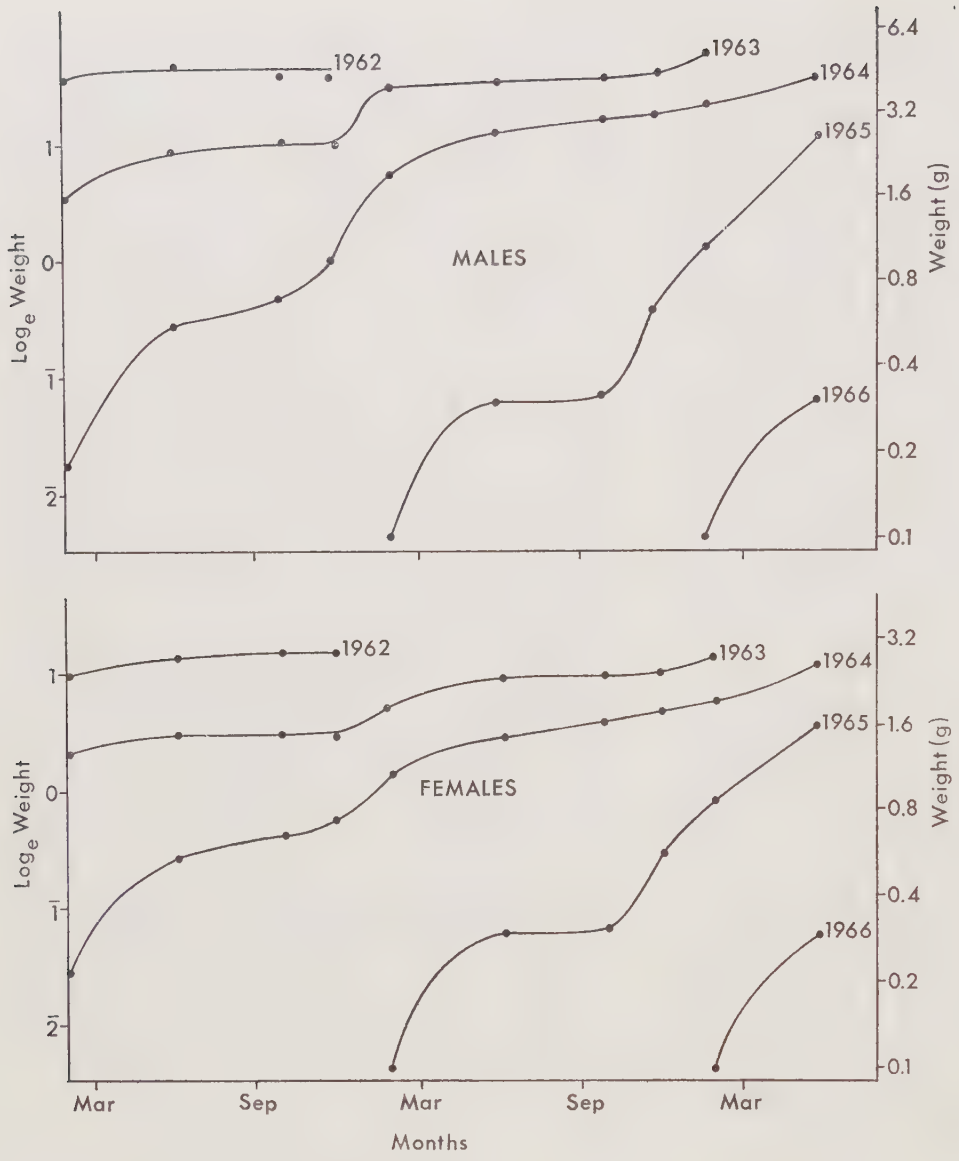

Fig. 5: Growth curves of bullies at station S1 plotted as log$_e$ weight against time. The years represent year classes.

trosimulium, are common members of the bottom fauna, but are rarely eaten.

The major food of all fish species is the mayfly *Deleatidium*, which formed 54 percent of all food organisms found and was present in 75 percent of all stomachs. Other major groups, however, are utilised in different proportions by different fish. Cased caddises (Sericostomatidae) and *Potamopyrgus* were eaten by trout and eels, but very rarely by bullies. *Coloburiscus*, *Hydropsyche*, and the Rhyacophilidae were eaten more by bullies and eels than by trout. Oligochaeta were taken mainly by eels. Chironomidae were of much greater importance to bullies than to either trout or eels. Food of terrestrial origin was rarely found in bullies or eels, but made up 5.4 percent of all food items in trout.

Table 19 takes no account of feeding differences between age classes, and gut contents of trout and bullies showed significant changes in diet with increasing age and size (tables 20 and 21).

Larvae of Chironomidae formed the major food of both trout fry and young bullies. Their importance declined with increasing fish size, though much more so in the trout than the bullies, being replaced among the older fish by *Deleatidium*. In general the small forms such as *Paracalliope* and chironomid larvae were of greatest numerical significance to the smaller trout and to bullies, and the larger trout increasingly took bigger food items and harder texture. The hard-cased Sericostomatidae, for example, were not eaten by trout fry and rarely by bullies, but were taken by larger trout and eels. Bulky animals such as the larger

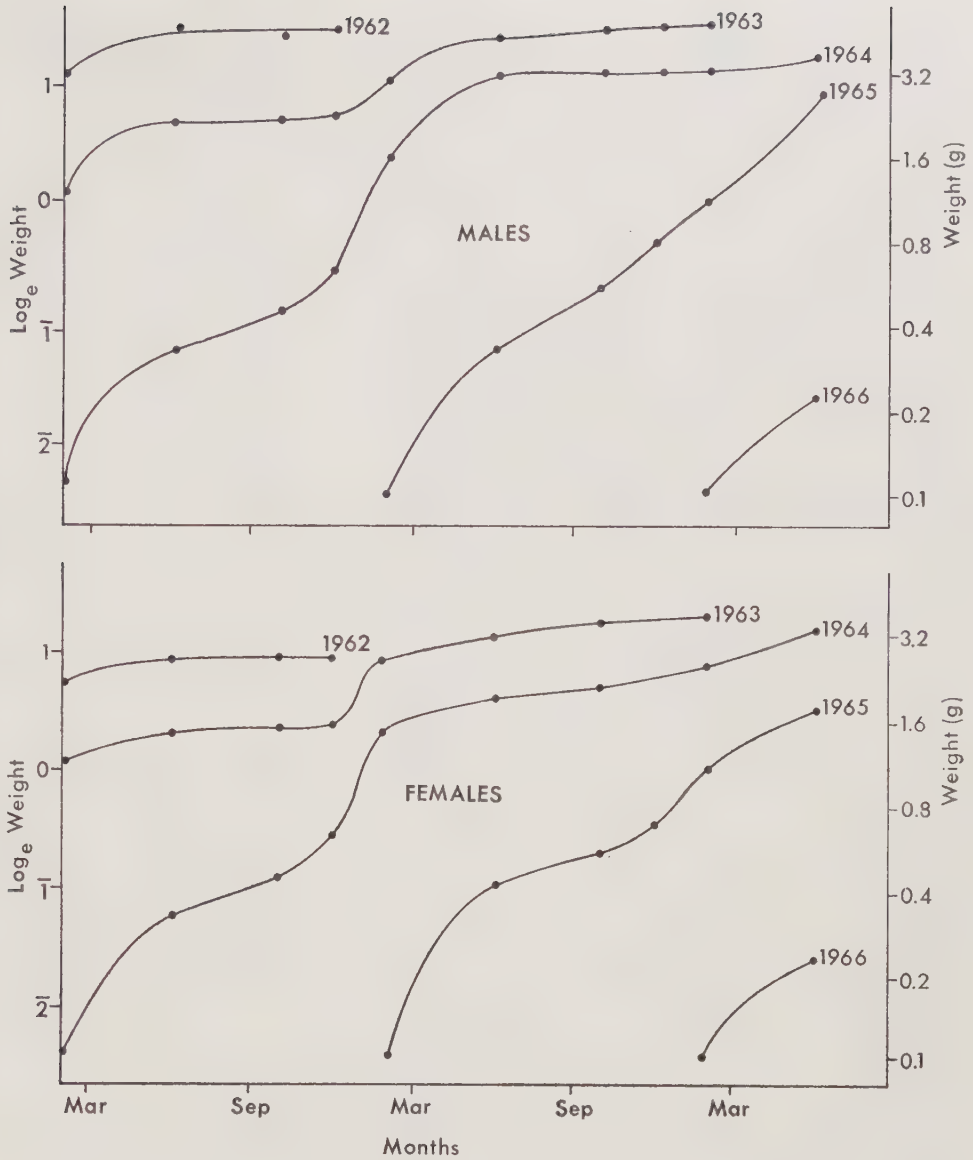

Fig. 6: Growth curves of bullies at station N1 plotted as log$_e$ weight against time. The years represent year classes.

Oligochaeta, *Stenoperla*, *Archichauliodes*, and fish were eaten only by eels and the largest trout fingerlings. Hopkins (1965) found that in fish of increasing size, represented by the series trout fry, adult *Philypnodon*, and eels, the size of Ephemeroptera eaten also increased. The same increase in size might be expected to apply to other food organisms of a wide size range. Indeed, the average weight of food organisms (*Deleatidium* and Chironomidae being omitted) in a series of juvenile trout was 0.5 mg in October fry, 1.1 mg in December, 2.1 mg in February, and 4.9 mg in June, which indicates a clear progression in size of food with increasing size of fish.

The largest aquatic food organisms available were crayfish (*Paranephrops*) and fish. Trout ate no crayfish, but about 8 percent of the eels contained crayfish remains. All but two of these eels were over 600 mm long, which indicated that total predation on crayfish was slight, since few eels were this size. This observation is also supported by the large numbers of crayfish found in both streams (table 6).

Fish appeared to be eaten no more frequently than crayfish. Small bullies were found in three trout of 117 mm, 119 mm, and 143 mm length. Of the 117 eels analysed in the early part of the programme, only two had eaten bullies and one a small trout. A sample of 18 selected large eels (564-1,150 mm long) yielded one more ingested bully and one ingested young eel.

Gravimetric

The percentage composition by weight of the food animals found in bullies, trout, and eels, as expected, gives larger organisms more prominence than do the

numerical results (tables 22-24). In eels particularly, ingested crayfish, bullies, and trout form most of the weight of food consumed. Since few eels contained these items, a second column in table 24 shows the percentage composition of food when eels containing fish and crayfish have been omitted. With this adjustment to the eel data, *Deleatidium* forms most of the food in all species of fish.

There is an important difference between numerical and gravimetric results for Chironomidae. Though trout fry and bullies eat large numbers of these larvae, the percentage composition by weight is very low compared with that of *Deleatidium*. The high assimilation (80 to 90 percent) (Ricker 1946) of soft-bodied animals, which include both *Deleatidium* and Chironomidae, indicates that the main nutrient supply, even of those fish feeding extensively on Chironomidae, still originated from the Ephemeroptera.

Table 19: Percentage Composition by Number (Comp.) and Percentage Occurrence (Occ.) of Animals Found in Bullies, Trout, and Eels

Food organism	Bullies		Trout		Eels	
	Comp.	Occ.	Comp.	Occ.	Comp.	Occ.
Aquatic						
Oligochaeta	x	2	x	3	5	8
Potamopyrgus	x	1	2	5	6	8
Latia	x	x	—	—	—	—
Ostracoda	x	x	x	x	—	—
Copepoda	x	1	—	—	—	—
Paracalliope	3	6	2	9	3	5
Paranephrops	—	—	—	—	x	8
Ameletopsis	—	—	—	—	x	2
Coloburiscus	2	6	x	3	7	15
Nesameletus	—	—	x	3	x	1
Deleatidium	50	75	57	87	51	36
Stenoperla	x	x	x	x	x	1
Zelandoperla	x	2	x	6	x	1
Archichauliodes	x	x	x	1	x	3
Sigara	—	—	x	2	—	—
Elmidae la.	x	x	1	5	—	—
Polycentropodidae	—	—	—	—	x	3
Sericostomatidae	x	2	6	16	7	12
Helicopsyche	—	—	x	1	—	—
Oxyethira	1	2	x	1	—	—
Hydropsyche	1	7	x	1	6	8
Rhyacophilidae	6	18	2	17	10	18
Austrosimulium	2	5	2	13	x	2
Chironomidae	33	40	27	43	3	9
Philypnodon eggs	x	x	—	—	—	—
Philypnodon	—	—	x	x	x	2
Salmo	—	—	—	—	x	1
Anguilla	—	—	—	—	x	1
Terrestrial						
Gastropoda (slugs)	x	x	—	—	—	—
Isopoda	x	x	x	x	—	—
Chilopoda	x	x	x	x	—	—
Ephemeroptera	—	—	2	1	—	—
Hemiptera	—	—	x	2	—	—
Coleoptera	—	—	x	x	x	1
Hymenoptera	—	—	x	1	—	—
Araneida	—	—	x	1	—	—
Total organisms	2,763		4,105		539	
Total fish	657		399		117	

x Less than 0.5 percent.
— Nil.

Daily Food Consumption

The analyses discussed above, though useful for comparative purposes and for revealing the proportions eaten of the various food organisms available, unfortunately give no guide to the amount consumed per unit time.

A number of authors have computed from laboratory experiments the daily food requirements of fish in terms of body weight and growth and have shown the desirability of separating two components, one of which contributes to general body maintenance (maintenance ration) and the other to increase in tissue (growth ration).

The maintenance ration in plaice (*Pleuronectes platessa* L.) is about 1 percent of body weight per day (Dawes 1931); in bluegills (*Lepomis macrochirus* Rafinesque) 1.7 percent (Ricker 1949); and in brown trout 1.2 percent (Pentelow 1939).

The growth ration is usually calculated from a conversion factor which can be applied to the growth increase of the fish to give the amount of food required for that increase. Bregnballe (1961), listing the results of several authors, quotes conversion factors between 3.7 and 5.8 for various flatfish (Heterosomata) and for rainbow trout (*Salmo gairdneri* Richardson). Bonham (1950) gives a figure of 3 for rainbow trout. Allen (1951), basing his work on that of Pentelow (1939), used 4.2 for brown trout. Burnet (1952a) used 4 in his study of the long-finned eel (*Anguilla dieffenbachi*).

Table 20: Percentage Composition by Number of Animals Found in Bullies of Two Age Groups

Food organism	First year			Second & third years		
	Oct	Feb	Jun	Oct	Feb	Jun
Aquatic						
Oligochaeta	1	1	2	x	1	1
Potamopyrgus	—	1	1	—	x	1
Latia	—	—	1	—	—	1
Ostracoda	2	—	x	—	—	—
Copepoda	—	2	x	—	x	—
Paracalliope	3	1	6	8	2	2
Coloburiscus	—	—	—	4	x	5
Deleatidium	32	26	43	61	58	48
Stenoperla	—	—	—	—	x	—
Zelandoperla	x	—	—	1	1	x
Archichauliodes	—	—	—	—	—	x
Elmidae la.	—	—	—	—	x	x
Sericostomatidae	x	1	—	—	x	1
Oxyethira	—	1	—	—	2	—
Hydropsyche	1	1	x	3	2	4
Rhyacophilidae	1	2	6	5	4	14
Austrosimulium	1	1	1	1	2	3
Chironomidae	58	63	39	16	27	19
Philypnodon eggs	—	—	—	—	x	—
Terrestrial						
Gastropoda (slugs)	—	—	—	—	—	x
Isopoda	—	—	—	—	—	x
Chilopoda	—	—	—	—	—	x

x Less than 0.5 percent.
— Nil.

Table 21: Percentage Composition by Number of Animals Found in Young Trout of Different Ages

Food organism	Oct Fry	Dec 3 months	Feb 5 months	Jun 8 months
Aquatic				
Oligochaeta	—	—	1	2
Potamopyrgus	—	—	x	x
Ostracoda	x	—	—	—
Paracalliope	6	x	x	x
Coloburiscus	x	—	1	1
Nesameletus	—	—	x	1
Deleatidium	24	71	67	68
Stenoperla	—	—	x	1
Zelandoperla	x	—	1	2
Archichauliodes	—	—	x	x
Sigara	—	—	1	—
Elmidae la.	—	1	1	—
Sericostomatidae	—	x	12	6
Helicopsyche	—	—	x	x
Oxyethira	—	—	x	—
Hydropsyche	x	—	x	1
Rhyacophilidae	1	3	3	5
Austrosimulium	—	5	3	2
Chironomidae	69	19	4	2
Philypnodon	—	—	—	x
Terrestrial				
Isopoda	—	—	—	—
Chilopoda	—	—	x	—
Ephemeroptera	—	—	x	5
Hemiptera	—	—	1	—
Coleoptera	—	—	x	x
Hymenoptera	—	—	x	—
Diptera	—	—	1	x
Araneida	—	—	x	—

x Less than 0.5 percent.
— Nil.

Table 22: Percentage Composition by Weight of Animals Found in Bullies of Two Age Groups

Food organism	First year Oct	Feb	Jun	Second & third years Oct	Feb	Jun
Aquatic						
Oligochaeta	9	7	6	x	12	1
Potamopyrgus	—	x	x	—	x	1
Latia	—	x	1	—	—	x
Ostracoda	x	—	x	—	—	—
Copepoda	—	x	x	—	x	—
Paracalliope	1	1	2	1	x	x
Coloburiscus	—	—	—	16	4	22
Deleatidium	81	62	64	68	77	50
Stenoperla	—	—	—	—	1	—
Zelandoperla	1	—	—	x	x	15
Archichauliodes	—	—	—	—	—	1
Elmidae la.	—	—	—	—	x	x
Sericostomatidae	x	2	—	x	x	x
Oxyethira	—	1	—	—	x	—
Hydropsyche	x	x	4	1	1	4
Rhyacophilidae	1	4	8	12	2	1
Austrosimulium	x	x	x	x	x	x
Chironomidae	6	22	4	x	1	x
Philypnodon eggs	—	—	—	—	x	—
Terrestrial						
Gastropoda (slugs)	—	—	—	—	—	2
Isopoda	—	—	—	—	—	x
Chilopoda	—	—	—	—	—	1

x Less than 0.5 percent.
— Nil.

Table 23: Percentage Composition by Weight of Animals Found in Young Trout of Different Ages

Food organism	Oct Fry	Dec 3 months	Feb 5 months	Jun 8 months
Aquatic				
Oligochaeta	—	—	8	4
Potamopyrgus	—	—	x	1
Ostracoda	x	—	—	—
Paracalliope	x	x	x	x
Coloburiscus	x	—	1	8
Nesameletus	x	—	x	x
Deleatidium	90	90	57	35
Stenoperla	—	—	5	4
Zelandoperla	1	—	x	x
Archichauliodes	—	—	x	1
Sigara	—	—	9	—
Elmidae la.	—	—	1	—
Sericostomatidae	—	x	6	7
Helicopsyche	—	—	x	x
Oxyethira	—	—	x	—
Hydropsyche	x	—	x	x
Rhyacophilidae	2	4	2	1
Austrosimulium	2	2	x	x
Chironomidae	4	2	1	x
Philypnodon	—	—	—	36
Terrestrial				
Isopoda	—	—	—	—
Chilopoda	—	—	x	—
Ephemeroptera	—	—	2	—
Hemiptera	—	—	5	x
Coleoptera	—	—	x	x
Hymenoptera	—	—	x	—
Diptera	—	—	x	x
Araneida	—	—	x	—

x Less than 0.5 percent.
— Nil.

Table 24: Percentage Composition by Weight of Animals Found in Eels

Food organism	All eels	Eels with fish and crayfish omitted
Aquatic		
Oligochaeta	1	7
Potamopyrgus	x	3
Paracalliope	x	x
Paranephrops	72	—
Ameletopsis	x	x
Coloburiscus	1	14
Nesameletus	x	x
Deleatidium	5	53
Stenoperla	x	1
Zelandoperla	x	x
Archichauliodes	x	1
Polycentropodidae	x	x
Sericostomatidae	x	1
Hydropsyche	1	14
Rhyacophilidae	x	3
Austrosimulium	x	x
Chironomidae	x	x
Philypnodon	4	—
Salmo	14	—
Terrestrial		
Coleoptera	x	x

x Less than 0.5 percent.
— Nil.

Table 25: Estimated Daily Food Consumption (g/sq m) of All Fish at S1 and N1 at Various Periods Between October 1965 and October 1966

	S1					N1				
	1965		1966			1965		1966		
	Oct	Dec	Feb	Jun	Oct	Oct	Dec	Feb	Jun	Oct
Trout	·172	·184	·128	·016	·032	·076	·144	·236	·016	·001
Bullies	·120	·072	·396	·152	·092	·060	·044	·444	·120	·112
Eels	·468	·312	·728	·372	·252	·796	2·372	1·096	1·308	1·196
Total	·760	·568	1·252	·540	·376	·932	2·560	1·776	1·444	1·309

In this range of unrelated fish the maintenance ration is evidently between 1 and 2 percent of body weight, and the conversion factor for growth lies between 3 and 6. Although these results are from fish in an artificial environment, several authors (for example, Allen 1951; Burnet 1952a; Horton 1961) have used them to estimate the daily requirements of fish in the natural environment, but such estimates are clearly approximations open to considerable error. Mann (1967) is of the opinion that though the growth conversion factors used by Allen and Horton are approximately correct for fish in middle life, they are too low for young fish. Gerking (1952), also, has shown that the efficiency of utilisation of protein for growth is greater in young fish than in old. The growth conversion factors mentioned above would therefore lead to over-estimates of food requirements. On the other hand, the data from which these figures were calculated were drawn from tank-living fish, whose metabolism might be expected to be at a lower level than that of fish in the wild.

A number of variables in the environment may affect the rate at which food is consumed and the efficiency with which it is utilised. Ricker (1946) discusses the findings of several authors from which it appears that temperature, age, and food availability can affect the efficiency of utilisation. Obviously, the type of food eaten must also be of importance in this respect. Under conditions of stress caused, for example, by high predator density, the maintenance ration will rise at the expense of the growth ration, which may introduce inconsistencies into any attempted calculation of total food requirements.

Despite such sources of error estimates of daily food consumption of the Hinaki fish population by use of the figures given above have been made.

The figures used by Allen (1951) for the trout of the Horokiwi Stream* have been used for the trout of the Hinaki, and since there are no other data, they have also been applied to the bullies. The daily maintenance ration has therefore been assumed to be 1.2 percent of body weight, and the growth ration has been calculated as 4.2 times the growth rate.

*Now designated as the Horokiri Stream by the New Zealand Geographic Board.

A different method has been used for the eels, as there was inadequate detail of the eel population structure. Burnet's (1952a) combined maintenance and growth conversion factor was used. This gives the total daily ration as a percentage of body weight, and for the Hinaki population this ranges between 2.18 and 2.30.

The food requirements of bullies have been calculated for each year class. This would have been desirable for the eels also, but since the data were not available, the average requirements for the whole population have been estimated. For the trout, of course, there was no necessity for class separation, since only one age group was present.

The growth rates of bullies and trout at the time of sampling have been calculated from plots of the natural logarithm of weight against time for successive samples. From the curve drawn by eye through the resultant points (fig. 2, 5, and 6) the instantaneous growth rate can be calculated for any short interval covering the sampling, and hence the mean growth in grammes per day can be determined for that interval.

The estimated food consumption per day at the time of sampling is shown for a year at stations S1 and N1 in table 25. For comparison with the bottom fauna figures (tables 4 and 5) the results are given in grammes per square metre.

Most of the food consumed by the total population is used by the eels, and the much larger population of eels at N1 is the reason for the greater consumption there. The quantities of food eaten by the other two species are fairly similar at both stations.

The trout, which inhabit the stream for only a short period of their lives and have a fairly prolonged period of high growth rate, initially eat much greater quantities of food than the resident bullies. The total biomass of trout present is always less than that of bullies and it follows, since the ratio of maintenance ration to body weight is assumed to be equal in both species, that the total maintenance requirement of the trout population is also less. The total food intake of the bullies surpasses that of the trout only with the development of the new year class of bullies in summer and the onset of down-stream migration of the trout.

Table 26: Standing Population of Fish and Bottom Fauna (g/sq m) at S1 and N1

	S1					N1				
	1965		1966			1965		1966		
	Oct	Dec	Feb	Jun	Oct	Oct	Dec	Feb	Jun	Oct
Trout	1·720	1·288	1·720	·432	·432	·860	1·288	3·440	·860	·860
Bullies	4·310	2·580	6·452	6·880	5·160	3·872	2·580	6·880	4·732	3·440
Eels	22·360	14·192	27·942	16·772	11·180	36·552	113·520	46·440	57·192	55·472
Total	28·390	18·060	36·114	24·084	16·772	41·284	117·388	56·760	62·784	59·772
Benthos	5·160	10·213	13·115	7·203	2·580	12·578	11·288	23·005	12·148	18·490

The food intake per day can be compared with the standing population of benthos at the time of sampling. Since very few crayfish were eaten, they can be omitted, so that table 25 can be directly compared with table 5. Total daily consumption by fish then appears to be about 5 to 20 percent by weight of the benthos.

The proportion of benthos consumed by fish does not appear to follow any pattern through the year. It is generally similar at both stations, though the weight and density of benthos at N1 are from 1.5 to 3.5 times greater than at S1. Since both bottom fauna populations are therefore supporting about the same proportion of fish predation, the availability of food may be partly controlling the fish population.

DISCUSSION

Larkin (1956) remarked that freshwater fish show comparatively little ecological specialisation and are flexible in their use of environmental resources. The niche occupied by a given species in a fish community varies according to the other species which share the environment. Because of this it is often difficult to see how species of a mixed fish population influence each other. Most authors seem to assume some degree of interspecific competition in such a situation, though Keast and Webb (1966) have shown that food specialisations and habitat preference restrict competition in complex fish faunas.

If direct predation is excluded, the three principal sources of interspecific competition among freshwater fish are: competition for spawning sites, for living space, and for food.

In the Hinaki fish community there can be no competition for spawning sites, since the breeding requirements of each species are completely dissimilar. There seems little likelihood of competition for living space except perhaps between the two species of eel, which appear to have similar requirements. There remains the possibility of competition for food.

The principal food source of all species of fish was the stream benthos. By comparison with figures given by Lagler (1956) the invertebrate fauna could be described as of "average richness" on the grading he used for North American streams. Both density and biomass of the Hinaki benthos surpassed those of the Horokiwi, which Allen (1951) considered to be similar to many New Zealand streams.

The principal items of food are more or less the same for all Hinaki fish, and all rely very largely on the mayfly genus *Deleatidium,* though fish may take this food from more than one source. Trout feed to a great extent on drifting animals, and bullies and eels search for food on the bottom. The size of food items taken depends partly on the gape of the fish (Thomas 1962), and larger fish accept larger prey. A mixed population of North American cyprinids commonly change their diet if a particular food runs short (Starrett 1950). Minor variations in the diet of each Hinaki species show that other prey animals are available and acceptable to the predator population if its main food is diminished. In point of fact, since *Deleatidium* remained the major food throughout the study, this mayfly was probably always abundant. The general impression is that there is little material competition for food among those species inhabiting the Hinaki system despite the general similarity of their diets.

Intraspecific competition on the other hand appears vigorous and may form a major mechanism of population control. The high mortality among the youngest bullies and trout and the different growth rates of trout in the Hinaki and Hinau are both likely to be density dependent (Foerster 1944; Nicholls 1958; Horton 1961) and caused by intraspecific rather than interspecific relations. Although interspecific predation may cause some mortality, it did not seem important in this study.

Ricker (1954) considers that density-dependent mortality has its greatest effect in the youngest members of the stock. Growth of the youngest Hinaki fish is probably also density dependent, becoming less so with maturity. Differences in trout growth rates are most obvious in the fry and early fingerling stage and are not significant later in the year.

Competition both for living space and food may be severe among dense populations of newly hatched fish. It is unlikely that a small stream can provide enough living space for the large increase at hatching. In the Hinaki two mechanisms may relieve this. Young trout become territorial very soon after leaving the redd (Kalleberg 1958) and lack of territory may cause high losses, as fish without established territories are removed from the system. Fry of bullies, on the other hand, do not appear to be territorial, but tend to shoal in quieter water. The gradual disappearance of the youngest year class from the sampling regions and its reappearance a year later may be due to population pressure forcing some young fish down stream. In the early summer there is a reverse movement of yearling bullies up stream. The reasons for this return have not been examined.

Competition for living space may affect growth. There is a large difference in growth rate between the Hinaki and Hinau trout populations during spring, the smaller population then having the higher growth rate. This suggests that trout at high density need a greater maintenance food ration, which reduces the amount of nutriment available for growth. This arises through greater energy expenditure in territorial defence in the high-density community. Such a situation can, of course, continue beyond the fry stage, but does not appear to do so here, possibly because the onset of migration reduces territorial fighting. Indeed, in summer fingerling trout shoal in the deeper pools.

Although competition for food cannot be demonstrated for the older fish, this probably happens among the younger stages, which do not eat as wide a range of food as the older and bigger fish. Starrett's observation referred to above does not therefore apply, and the food supply of the youngest bullies and of trout is more limited than it is for the older fish. This situation is aggravated by the large size of the young

population. Nikolsky (1963) observed that the growth rate of fish becomes more variable in a population suffering food shortage. This finding has adaptive value in that the greater size range of the predators allows differences in the size range of food items to appear in the same year class. Wide variability in size has not been noted in the young trout, but is obvious among the 0+ class bullies. In fact, in this year class there is evidence in some samples of a polymodal distribution of length frequency arising, presumably, from differences in time of hatching. The breeding season of the adult bullies in any case is fairly long (October to December) and must inevitably give rise to a year class of large size range. This phenomenon may indicate an adaptation which allows greater utilisation of food resources that otherwise might be severely restricted.

Among adults the main intraspecific competition is for spawning space. The study was not designed to estimate the maximum breeding population that could be supported, but it is evident that in both trout and bullies some control of the succeeding generation will be afforded by the space available in the streams for spawning. The eels, of course, do not breed in fresh water.

In the larger of the two spawning runs of trout there were only 73 fish (36 females) divided between the two streams. With about 2.5 km of what appeared to be good spawning ground a greater number of fish could certainly have spawned successfully. It is not known whether the same can be said for the bullies. The size of the spring breeding population is large for what the author believes is suitable breeding ground. However, it is difficult to gauge the exact requirements for nesting; territorial defence behaviour may limit the number of possible nesting sites more than the physical environment does (Ricker 1954). It seems likely that some competition for sites takes place between breeding males and that most of the available sites are utilised.

The total daily consumption of food by fish, 5 to 20 percent by weight of the standing benthic population, represents a high rate of cropping, and obviously to support this predation new material must appear regularly in the food supply. Adults of several insect groups, particularly species of *Deleatidium* and Chironomidae, occur at all times of the year, which implies more or less continuous reproduction among those groups most heavily predated, and this therefore provides one source of new material. It has been pointed out by Illies (1959) and Hynes (1961) that some aquatic insects undergo delayed hatching, so that new larvae are added over prolonged periods. This has been quoted as an adaptation which allows better use of restricted living space, but it also serves to replace those lost by predation.

SUMMARY

The population density, growth, and food have been described for the members of a mixed population of juvenile brown trout, bullies, and eels. The data presented have been used to examine the ecological and competitive food relations of these species.

The food of all species of fish was the stream benthos, and most of the animals eaten belonged to the Ephemeroptera and Trichoptera. The invertebrate fauna was of "average richness" on the grading used for North American streams and in both density and biomass surpassed that of the Horokiwi, which has been considered to be similar to many New Zealand streams.

A consideration of the daily food requirements of the fish and the availability of food led to the conclusion that under normal conditions food was not a limiting factor among the adults and large juveniles. There seemed little interspecific competition for food, for living space, or for spawning sites.

It was considered that predation by larger fish on smaller was insignificant. Yet 90 percent of young bullies and trout were lost during the first few months of life; so intense intraspecific competition among very young fish was postulated. During the period of highest mortality these young fish were present in large numbers, shared the same food requirements, and apparently ate a limited variety of food items. Under these conditions the availability of food and of living space were probably the principal factors governing their survival.

There appeared to be several mechanisms operating among the young fish to reduce the likelihood of a general food shortage. Among the trout fry, territorial behaviour ensured dispersal of fish and reduced feeding pressure. Among bully fry, which showed no obvious territorialism, there was evidence of migration by some members down stream from the breeding area; moreover the protracted breeding season gave rise to a year class of large size range which might be expected to eat a wide range of food.

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